



1 **Competing effects of seasonal hydrodynamics and** 2 **temperature-dependent development shape marine larval** 3 **dispersal**

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10 **Abstract (350 words)**

11 Marine larval dispersal emerges from the interaction between physical transport and biological
12 development. Yet biophysical dispersal models commonly prescribe pelagic larval duration
13 independently of the thermal histories experienced by larvae, potentially overlooking an important
14 coupling between environmental conditions, development, and transport. This simplification may be
15 particularly consequential for species with prolonged spawning seasons, because larvae released at
16 different times encounter distinct circulation regimes and thermal environments. Here, using Japanese
17 anchovy (*Engraulis japonicus*) as a case study, we coupled a Lagrangian particle-tracking model with
18 two representations of temperature-dependent larval development, a growing degree-day (GDD)
19 approach and an optimal growth temperature (OGT) approach, to examine how physical transport and
20 biological development jointly shape larval dispersal. A fixed 30-day travel duration was simulated to
21 isolate seasonal variation in hydrodynamic transport. Larvae released from Haizhou Bay on six dates
22 between May and July during 2013–2018 experienced markedly different trajectory-specific thermal
23 histories, resulting in substantial variation in development-dependent travel duration. Under the fixed-
24 duration scenario, median dispersal distance increased from 128.2 km on 1 May to 168.8 km on 15 July,
25 indicating progressively stronger hydrodynamic transport over the spawning season. In contrast, the
26 GDD approach predicted a decrease in travel duration from 62.1 to 25.5 d and a corresponding decrease



in median dispersal distance from 226.5 to 154.2 km, reversing the hydrodynamically driven seasonal trend. The OGT approach produced a nonlinear seasonal response because larval growth declined when experienced temperatures exceeded the thermal optimum, further demonstrating that the thermal–development relationship can qualitatively alter predicted dispersal patterns. Together, these results demonstrate that larval dispersal emerges from competing physical and biological controls, with spawning phenology coupling the two by simultaneously altering seasonal circulation and trajectory-specific thermal histories. Representing travel duration as an environmentally responsive biological trait, rather than a fixed parameter, may therefore improve predictions of larval dispersal and population connectivity under climate-driven shifts in spawning phenology. More broadly, our findings suggest a spatial dimension to the phenological match–mismatch framework, whereby shifts in spawning phenology may alter not only when larvae encounter suitable conditions but also where these encounters occur.

Keywords

Larval dispersal; physical–biological coupling; spawning time; temperature-dependent development; Lagrangian particle tracking

1. Introduction

Larval dispersal, the transport of larvae away from their source populations, is a fundamental process shaping individual fitness, population connectivity, and the persistence and productivity of marine populations (Almany et al., 2017; Cowen and Sponaugle, 2009). Because many marine species experience a pelagic larval stage, larvae may be transported over substantial distances before recruiting to suitable habitats, thereby connecting spatially separated populations (Cowen and Sponaugle, 2009; Faillettaz et al., 2018; Sato et al., 2023; Wood et al., 2013). Larval dispersal emerges from the interaction between physical transport and biological development (Shi et al., 2026b). Physical transport, governed primarily by ocean circulation and modified by larval behaviour, determines the velocity and direction of movement, whereas biological development determines how long larvae remain in the dispersive stage. These controls are inherently coupled because larval development is strongly temperature dependent, while the temperatures experienced by larvae depend on their trajectories through spatially and temporally heterogeneous marine environments. Hydrodynamic transport therefore determines not only



56 where larvae move, but also the thermal histories they experience and, consequently, how long they
 57 remain subject to transport.

58 Despite this physical–biological coupling, biophysical particle-tracking models commonly
 59 prescribe pelagic larval duration as a fixed parameter (Ayata et al., 2010; Burgess et al., 2021; Chaput et
 60 al., 2022; Huret et al., 2010; Majoris et al., 2019; Saito et al., 2026; Suhaemi et al., 2026; Takeshige et
 61 al., 2015; Xing et al., 2021). This simplification effectively decouples biological development from the
 62 environmental conditions experienced during dispersal. In reality, larvae following different trajectories
 63 may encounter substantially different temperatures and therefore develop at different rates, even when
 64 released from the same spawning population (Shi et al., 2026b). Previous studies have separately
 65 demonstrated the effects of spatial variation in temperature, ocean circulation, spawning location, and
 66 spawning time on larval dispersal (Ayata et al., 2010; Hinrichsen et al., 2012; Lu et al., 2023; O'connor
 67 et al., 2007; Shi et al., 2026d). However, the consequences of trajectory-specific thermal histories for
 68 larval development and their interaction with seasonal hydrodynamic transport remain poorly understood.
 69 This distinction is important because environmentally driven changes in development can alter the
 70 duration over which larvae are transported and may therefore reinforce or counteract changes in physical
 71 transport. Consequently, seasonal changes in larval dispersal cannot necessarily be inferred from
 72 hydrodynamic variability alone.

73 Spawning phenology provides a natural context in which these physical and biological controls
 74 interact. Species with prolonged spawning seasons release larvae into seasonally varying circulation and
 75 thermal environments. Changes in circulation alter transport velocity and direction, while changes in
 76 temperature regulate developmental rates and hence the duration of dispersal (Fig. 1). Importantly, larval
 77 development depends on the temperatures experienced along individual trajectories rather than solely on
 78 conditions at spawning locations (Shi et al., 2026b). Spawning phenology can therefore influence
 79 dispersal through a dynamic coupling among seasonal circulation, trajectory-specific thermal exposure,
 80 and biological development. This mechanism may become increasingly important under climate change
 81 because spawning and other early-life phenological events are shifting in many marine fishes (Asch,
 82 2015; Asch et al., 2019). Such shifts have primarily been considered within the match–mismatch
 83 framework, whereby asynchronous phenological responses of fish and their prey can alter recruitment.
 84 However, if spawning phenology also modifies dispersal through temperature-dependent development,
 85 phenological shifts may affect not only when larvae encounter suitable prey and nursery conditions, but



also where these interactions occur.

Here, we use Japanese anchovy (*Engraulis japonicus*) in Haizhou Bay and the adjacent China Seas as a case study to investigate how seasonal hydrodynamics and temperature-dependent development jointly shape marine larval dispersal. Japanese anchovy has a prolonged spawning season (Zhang et al., 2020), exposing larvae to pronounced seasonal variability in both circulation and temperature. We coupled a Lagrangian particle-tracking model with two alternative representations of temperature-dependent development: a growing degree-day (GDD) approach representing cumulative thermal exposure (Neuheimer and Taggart, 2007; Shi et al., 2026b) and an optimal growth temperature (OGT) approach (Takasuka et al., 2007) representing a nonlinear thermal–growth relationship. Larvae were released on six dates between May and July during 2013–2018, and their travel durations were determined from temperatures experienced along individual trajectories. A fixed 30-day travel duration was additionally simulated as a hydrodynamic baseline to isolate seasonal changes in physical transport. Specifically, we examined how spawning phenology alters trajectory-specific thermal histories and development-dependent travel durations, and whether these biological changes reinforce or counteract seasonal variation in hydrodynamic transport to shape larval dispersal.

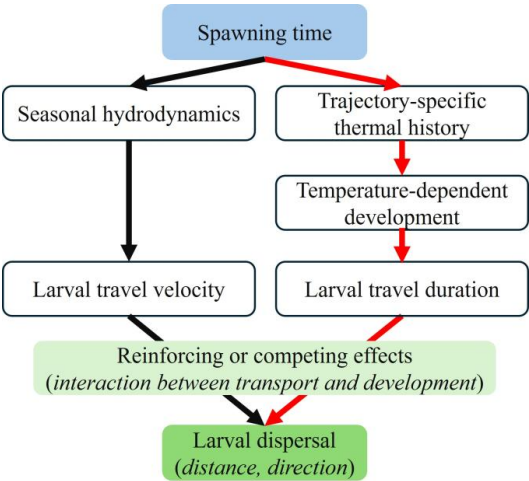


Figure 1. Conceptual framework of the coupled physical and biological controls on larval dispersal.

2. Materials and Methods

2.1. Study Species and Area

Japanese anchovy (*Engraulis japonicus*) is one of the most abundant pelagic fish species in the



106 Yellow Sea and plays a key trophic role in its marine ecosystem (Zhao et al., 2003). The egg stage was
107 not included in the dispersal simulations because embryonic development lasts only approximately 42–
108 72 h, resulting in relatively limited transport before hatching compared with the subsequent larval stage
109 (Takeshige et al., 2015; Xing et al., 2020). Japanese anchovy larvae begin to develop swimming ability
110 at body lengths of approximately 5–7 mm, with swimming performance increasing during development
111 and becoming more pronounced at 20–25 mm (Masuda, 2011). Here, we focused on the early larval stage
112 from hatching to a standard length of 20 mm. Active swimming was intentionally excluded to isolate the
113 effects of hydrodynamic transport and temperature-dependent development on larval dispersal. Larvae
114 were therefore represented as passive particles, providing a mechanistic baseline for examining physical–
115 biological coupling rather than a complete representation of realized larval movement. This assumption
116 is also consistent with previous particle-tracking studies of Japanese anchovy larvae (Takeshige et al.,
117 2015; Xing et al., 2020). Previous particle-tracking studies assumed a fixed larval travel duration of either
118 30 d (Takeshige et al., 2015) or 60 d (Xing et al., 2020). In contrast, this study estimated larval travel
119 duration dynamically based on the water temperatures experienced along individual larval trajectories.
120 Here, travel duration refers to the simulated period from release to the developmental endpoint of 20 mm
121 and represents the duration over which larvae remain subject to dispersal in the model.

122 Haizhou Bay (HZB), located along the western margin of the Yellow Sea, is an important spawning
123 ground for Japanese anchovy (Zhang et al., 2022) and was therefore selected as the larval release region
124 for the particle-tracking simulations (Fig. 2). Its prolonged spawning season exposes larvae released at
125 different times to pronounced seasonal variability in both hydrodynamic and thermal conditions,
126 providing a suitable case study for examining how spawning time influences larval dispersal through
127 coupled physical transport and temperature-dependent development.

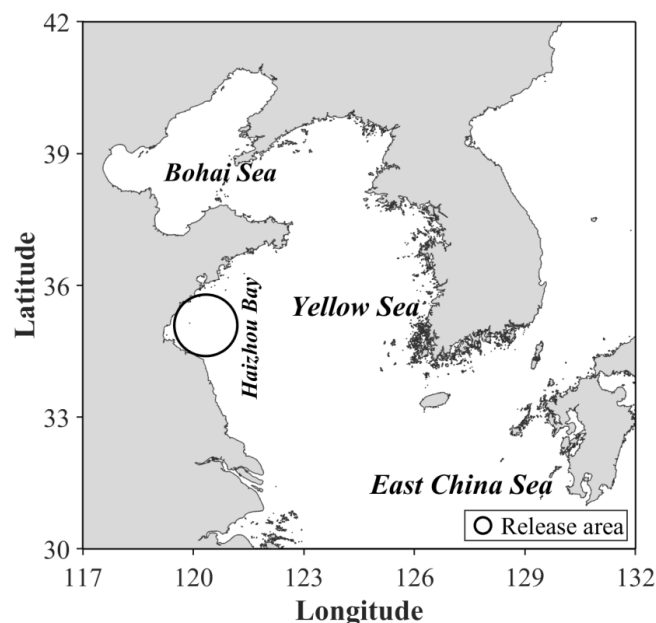


Figure 2. Haizhou Bay (HZB), one of the major spawning grounds of Japanese anchovy (*Engraulis japonicus*) in the Yellow Sea, and the larval release area used in the particle-tracking simulations (black circle). White indicates ocean and grey indicates land.

2.2. Hydrodynamic Model

Hydrodynamic outputs from the Finite-Volume Community Ocean Model (FVCOM) for the period 2013–2018, originally developed by Xing et al. (2020) to investigate larval retention of Japanese anchovy in the China Seas, were used in this study. The model generated hourly, three-dimensional hydrodynamic fields covering the Bohai Sea, Yellow Sea, and East China Sea from 1987 to 2018. The computational domain was discretized using an unstructured triangular mesh consisting of 86,107 elements and 44,682 nodes, with an average horizontal resolution of approximately 6.5 km. Vertically, the water column was represented by 41 terrain-following sigma layers, allowing for realistic simulation of vertical stratification and shear. The uppermost sigma layer of FVCOM model was used as Japanese Anchovy have typically been found near the surface (Iseki and Kiyomoto, 1997). Further details on model configuration and validation are available in Xing et al. (2020).

2.3. Lagrangian Particle Tracking Model



144 A two-dimensional Lagrangian particle-tracking model was developed in MATLAB® based on
 145 SWIM v2.0 to simulate larval dispersal trajectories (Shi et al., 2026a). The particle-tracking code and
 146 simulation outputs generated in this study are publicly available through Zenodo
 147 ([10.5281/zenodo.21358003](https://doi.org/10.5281/zenodo.21358003)). Earlier versions of SWIM have been successfully applied in a variety of
 148 ecological applications, including forward-in-time simulations of silver eel (*Anguilla rostrata* and *A.*
 149 *anguilla*) migration (Béguer-Pon et al., 2016), walleye (*Sander vitreus*) larval dispersal under passive
 150 and active swimming scenarios (Shi et al., 2026c) backward-in-time estimation of Lake Whitefish
 151 (*Coregonus clupeaformis*) hatching locations in Lake Erie (Shi et al., 2024), and backward-in-time
 152 reconstruction of walleye larval age and hatching sites using a growing-degree-day approach (Shi et al.,
 153 2026b).

154 Diel vertical migration was not included in the present simulations; given that anchovy eggs are
 155 positively buoyant and typically aggregate in the uppermost water column (Iseki and Kiyomoto, 1997),
 156 all simulated particles were constrained to the surface layer and initialized with a uniform horizontal
 157 distribution across the designated release area. For boundary condition, any particle advected into
 158 nearshore coastal zones with water depths shallower than 6 meters was immediately classified as stranded
 159 or dead, effectively terminating its tracking trajectory (Lett et al., 2008). The particle-tracking model was
 160 integrated using a time step of 10 min (600 s), whereas FVCOM hydrodynamic fields were available at
 161 hourly intervals. To reconcile these temporal resolutions, velocity and temperature fields at each particle
 162 location were obtained by linearly interpolating between consecutive hourly FVCOM outputs. Particle
 163 positions were then updated every 10 min using the interpolated flow fields, together with a random-
 164 walk diffusion component representing sub-grid-scale turbulent mixing. The horizontal diffusion
 165 coefficients were set to $K_x = K_y = 0.1 \text{ m}^2 \text{ s}^{-1}$. The specific configuration for larval release and tracking
 166 is detailed as follows:

167 **Larval release location:** The simulated release domain was restricted exclusively to the Haizhou
 168 Bay (HZB) spawning ground. To ensure spatial uniformity, particles were released within a circular
 169 geographical boundary centered at 120.34°E, 35.09°N, with a radius of approximately 77.8 km. Within
 170 this specific zone, 20,000 independent particles were randomly generated per release event. A sensitivity
 171 analysis was conducted to ensure that the number of released particles was sufficient to produce robust
 172 simulation results (Fig. S1).

173 **Larval release time:** To capture the seasonal and interannual variability of the coastal circulation



174 during the peak reproductive period, particles were released across six consecutive years (2013–2018).
 175 Within each year, release events occurred biweekly across six specific temporal nodes: May 1st, May
 176 15th, June 1st, June 15th, July 1st, and July 15th. This experimental design yielded a total of 720,000
 177 $(20000 \times 6 \times 6)$ tracked particles throughout the study period.

178 **Larval travel duration:** Rather than adopting a fixed travel duration, this study implemented a
 179 biologically based settlement criterion to account for spatial and temporal variability in larval growth
 180 conditions. Specifically, travel duration was defined as the time required for a larva to reach 20 mm in
 181 standard length. Because larval growth is temperature dependent, the growth rate of each individual was
 182 determined by the water temperatures experienced along its dispersal trajectory. Consequently, neither
 183 the growth rate nor the required travel duration could be specified a priori. Two approaches, described
 184 below, were used to estimate the time required for each larva to grow to 20 mm.

185 **2.4. Larval Dispersal Travel duration**

186 **(1) Growing Degree-Day (GDD) Approach**

187 The development of Japanese anchovy larvae was quantified using a growing degree-day
 188 (GDD; °C·day) approach. GDD on day t was computed as:

$$189 \quad GDD(t) = \sum_{i=1}^t (T_i - T_0) \cdot \Delta d \quad (1)$$

190 where T_i is the local water temperature experienced by a larva on day i . Because the particle-tracking
 191 model used a 10-min time step, each day consisted of 144 simulation steps. Therefore, T_i was calculated
 192 as the mean water temperature experienced by the larva across all 144 steps within that day. T_0 is the
 193 biological base temperature, which was set as 12.0 °C (Zhang et al., 2022). When $T_i < T_0$, the term
 194 $T_i - T_0$ was set to zero. Δd is the time increment (1 day).

195 Laboratory rearing experiments have shown that Japanese anchovy larvae reach a body length of
 196 20 mm after 32 days of development at a constant temperature of 23.2 °C (Masuda, 2011). Consequently,
 197 the cumulative thermal requirement for larvae to attain 20 mm was estimated as $(23.2-12) \times$
 198 $32=358.4$ °C·day. Therefore, the modeled travel duration t_g , was determined as the time required for a
 199 larva to accumulate the thermal units necessary to reach 20 mm in length. Specifically, t_g was
 200 determined as the first day (m) at which the GDD exceeded 358.4 °C·day:

$$201 \quad t_g = m, \text{ when } \sum_{i=1}^m (T_i - T_0) \cdot \Delta d \geq 358.4 \quad (2)$$

202 **(2) Optimal Growth Temperature (OGT) Approach**



Alternatively, Takasuka et al. (2007) derived an empirical relationship between the recent 3-day mean growth rate of larval Japanese anchovy and sea surface temperature:

$$y = -2.302 + 0.255x - 0.006x^2 \quad (n=34, r^2=0.507, p<0.001) \quad (3)$$

where y is the daily growth rate ($\text{mm} \cdot \text{day}^{-1}$) and x is the sea surface temperature ($^{\circ}\text{C}$). This relationship was developed from 34 samples comprising 2,041 Japanese anchovy larvae collected at 50 stations spanning inshore to offshore waters of the western North Pacific between 1990 and 2004. The larvae ranged from 6.4 to 34.3 mm in standard length, and sea surface temperature was measured concurrently with larval sampling.

In this research, the standard length at hatching (L_0) was assumed as 3 mm (Togoshi et al., 2024). During dispersal, the daily growth increment of each larva was determined by the local water temperature experienced along its trajectory. To avoid biologically unrealistic negative growth under low-temperature conditions, daily growth rates were constrained to be non-negative. Larval standard length at day (t) was therefore calculated as:

$$L(t) = L_0 + \sum_{i=1}^t (-2.302 + 0.255T_i - 0.006T_i^2) \quad (4)$$

where L represents the larval standard length at day t . The travel duration t_d computed using this approach was determined at the day when L exceeded 20 mm.

The two approaches were not intended to identify a single best representation of Japanese anchovy growth, for which region-specific temperature–growth relationships remain uncertain. Instead, they were used as alternative representations of thermal control on development to evaluate whether the influence of temperature-dependent development on dispersal depends on the form of the thermal–development relationship.

(3) Fixed Travel Duration (30 d)

To separate seasonal changes in hydrodynamic transport from those associated with temperature-dependent development, we conducted an additional set of simulations in which all particles were tracked for a fixed duration of 30 d, following Takeshige et al. (2015). Because particles released on different dates were advected by the corresponding time-varying hydrodynamic fields but shared the same travel duration, differences among release dates in this scenario primarily represent seasonal variation in hydrodynamic transport. We therefore used the fixed-duration simulations as a hydrodynamic baseline against which the GDD- and OGT-based simulations were compared. Differences between the temperature-dependent and fixed-duration simulations quantify the influence of development-dependent



233 variation in travel duration on predicted dispersal.

234 **2.5. Larval Dispersal Pattern and Distance**

235 Using the travel durations derived above (t_g and t_d), larval settlement locations were determined
 236 by terminating each simulated larval trajectory at the corresponding travel duration. Settlement density
 237 was calculated for each grid cell by dividing the number of settled larval particles within the cell by the
 238 total number of particles settled. Dispersal distance was determined as the straight-line distance between
 239 each particle's release and settlement locations. Median dispersal distance was defined as the distance
 240 below which 50% of larvae settled, whereas long-distance dispersal was represented by the 95th
 241 percentile, below which 95% of larvae settled.

242 **3. Results**

243 **3.1. Spawning Time Alters Trajectory-Specific Thermal Histories**

244 Larvae experienced markedly different thermal environments among release dates but relatively
 245 consistent temperatures among release years. Fig.3 shows the local water temperatures larvae
 246 experienced along their movement trajectories within travel duration. For example, the dark solid blue
 247 line in Fig. 3a, increased from approximately 12.4 to 22.1 °C, represents the mean temperature
 248 experienced by the 20,000 larvae released on May 1 over 6 years, under the GDD approach. Release date
 249 had a significant effect on the temperatures experienced by larvae ($p < 0.01$; Table S1). Specifically, the
 250 mean temperature on the first day after release increased from 12.4 to 24.3 °C as the release date shifted
 251 from May 1 to July 15. Release year had no significant effect on the temperatures experienced by larvae,
 252 with the exception of 2017 ($p > 0.01$).

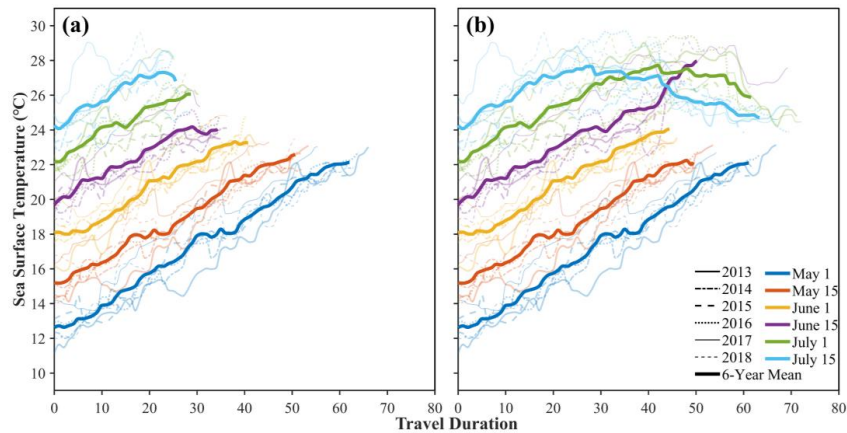


Figure 3. Local water temperatures *E. japonicus* larvae experienced along their movement trajectories within travel durations, estimated using the (a) Growing Degree-Days (GDD) approach and (b) Optimal Growth Temperature (OGT) approach. Different line styles represent different release years, while the thickest line indicates the 6-year mean water temperature experienced by larvae.

3.2. Thermal Histories Regulate Larval Travel Duration

Spawning-time shifts in thermal history produced either monotonic or nonlinear changes in travel duration depending on the form of the temperature–development relationship.

3.2.1. Growing Degree-Day (GDD) Approach

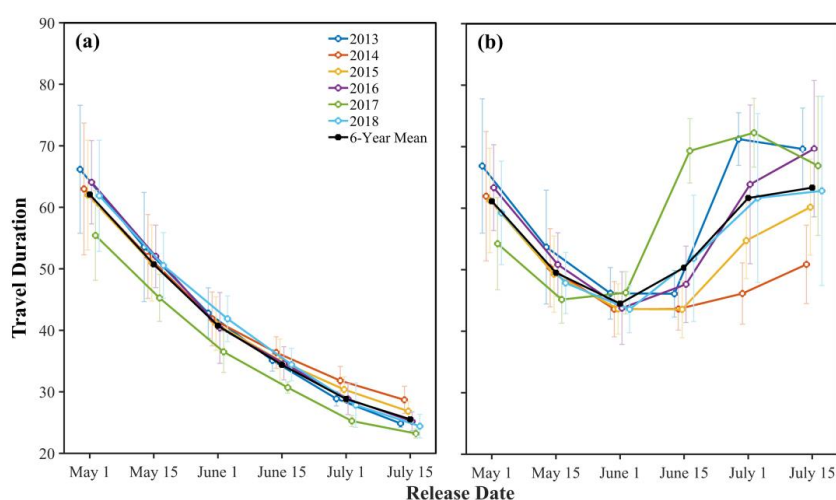
Using the GDD approach, modeled larval travel durations (t_g) decreased monotonically with later release dates (Fig. 4a). As surface water temperatures increased from May to July, the time required to accumulate the physiological settlement threshold (358.4 °C·day) shortened significantly (Fig. 3a). A pronounced difference was observed between early-spring and midsummer cohorts: travel durations ranged from approximately 55 to 66 days for larvae released on May 1, compared with 23–29 days for those released on July 15, indicating a 2.2- to 2.7-fold acceleration in development. Overall, travel durations were shorter in 2017 than in the other years, suggesting that summer water temperatures in the Yellow Sea were higher in 2017. This finding is consistent with the observations of Shi and Zhao (2026).

3.2.2. Optimal Growth Temperature Approach

Unlike the GDD approach, the OGT approach produced a nonlinear, “U-shaped” relationship between travel duration (t_d) and release date (Fig. 4b), with the turning point generally occurring around



273 June 1. Travel duration decreased with later release dates before this point but increased thereafter. This
 274 pattern can be explained by Equation 3: larval growth rate increases with water temperature up to
 275 21.25 °C while decreases at higher temperatures. After June 1, larvae experienced temperatures above
 276 21.25 °C along most of their trajectories (Fig. 3), resulting in slower growth and longer travel durations.
 277 Using this approach, the longest travel duration remained approximately 1.4–1.6 times the shortest
 278 duration.



279
 280 **Figure 4.** Simulated travel durations of *E. japonicus* larvae prior to settlement (2013–2018) using two
 281 approaches: (a) the Growing Degree-Days (GDD) approach, and (b) Optimal Growth Temperature (OGT)
 282 approach.

283 3.3. Effects of Temperature-Dependent Travel Duration on Larval Dispersal

284 The effect of temperature-dependent travel duration on dispersal was isolated by comparing
 285 simulations initiated from the same location and release date but using different travel-duration
 286 formulations. Because these larvae were exposed to the same hydrodynamic fields, differences in their
 287 dispersal patterns and distances can be attributed solely to temperature-dependent variation in larval
 288 development and the resulting travel duration, rather than to differences in hydrodynamic forcing. For
 289 example, for larvae released on May 1, the six-year mean travel durations estimated using the GDD and
 290 OGT approaches were similar (62.1 and 61.1 d, respectively; Table 1). Consequently, the settlement
 291 centroids (Fig. 5), density distributions (Fig. 6), mean median dispersal distance (MDD), and long-



distance dispersal (LDD) (Table 1) were also similar between the two approaches. Likewise, for larvae released on July 1, the mean travel duration estimated using the GDD approach was 28.8 d, close to the fixed duration of 30 d, resulting in similar dispersal metrics between the GDD and fixed 30-d approaches. In contrast, for larvae released on July 15, the estimated travel durations differed substantially between the GDD and OGT approaches (25.5 versus 63.3 d, respectively), resulting in pronounced differences in all of these dispersal metrics. Overall, using all three travel-duration scenarios, the centroids of settled larval particles were located northeast of the release site and clustered near 36°N for most release events (Fig. 5).

3.4. Effects of Seasonal Hydrodynamic Transport on Larval Dispersal

Seasonal effects on hydrodynamic transport were evident even when travel duration was similar. For example, under the OGT approach, the modeled travel durations for larvae released on May 1 and July 15, 2015, were nearly identical (approximately 62 d); nevertheless, their dispersal patterns and settlement centroid locations differed markedly (Figs. 5 and 6), indicating the influence of seasonal changes in hydrodynamic conditions on larval travel velocity and, consequently, dispersal. This effect was further demonstrated using the fixed 30-d travel duration, which eliminated variation in travel duration among release dates. Despite the identical travel duration, MDD and LDD generally increased with later release dates (Table 1). These results demonstrate that seasonal variation in hydrodynamic conditions associated with spawning time can independently alter larval travel velocity and, in this case, increase dispersal distances.

3.5. Combined Effects of Temperature-Dependent Travel Duration and Seasonal Hydrodynamics on Larval Dispersal

Comparing larval dispersal patterns and distances among release dates within either the GDD or OGT approach reveals the combined effects of spawning time on both the thermal histories experienced by larvae and the seasonal hydrodynamic conditions governing their transport. Under the GDD approach, MDD and LDD decreased nearly monotonically with later release dates (Table 1). This trend was opposite to the nearly monotonic increase in MDD and LDD obtained using the fixed 30-d travel duration, under which the effect of temperature-dependent variation in travel duration was removed. The contrasting trends indicate that the effects of spawning time mediated through thermal histories and temperature-dependent travel duration counteracted those mediated through seasonal hydrodynamics.



Specifically, although seasonal hydrodynamic conditions tended to increase dispersal distances for later-spawned larvae, warmer thermal conditions associated with later spawning accelerated larval development and shortened travel duration, thereby limiting the time available for transport and ultimately reducing dispersal distances under the GDD approach.

A similar interaction was evident under the OGT approach. However, because OGT-derived travel durations exhibited a nonlinear seasonal pattern from those estimated using the GDD approach, the resulting MDD and LDD did not show the same monotonic decrease with later release dates. Instead, their variation among release dates reflected the balance between changes in temperature-dependent travel duration and seasonal hydrodynamic conditions. Together, these results demonstrate that the effect of spawning time on larval dispersal cannot be explained by either thermal conditions or hydrodynamics alone; rather, the observed dispersal patterns emerge from their combined—and potentially opposing—effects on larval travel duration and velocity. These substantial differences demonstrate that assuming a constant travel duration can substantially misrepresent larval dispersal by neglecting temperature-dependent variation in larval development associated with spawning time.

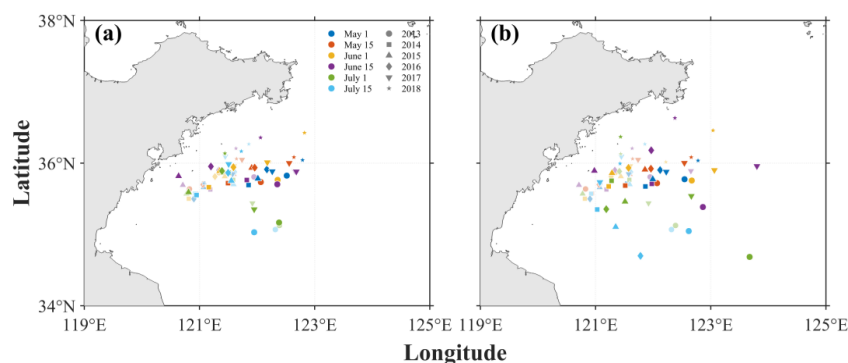


Figure 5. The centroid distribution of different release events, using (a) GDD approach and (b) OGT approach. The centroids derived from the 30 days are indicated in lighter colors.

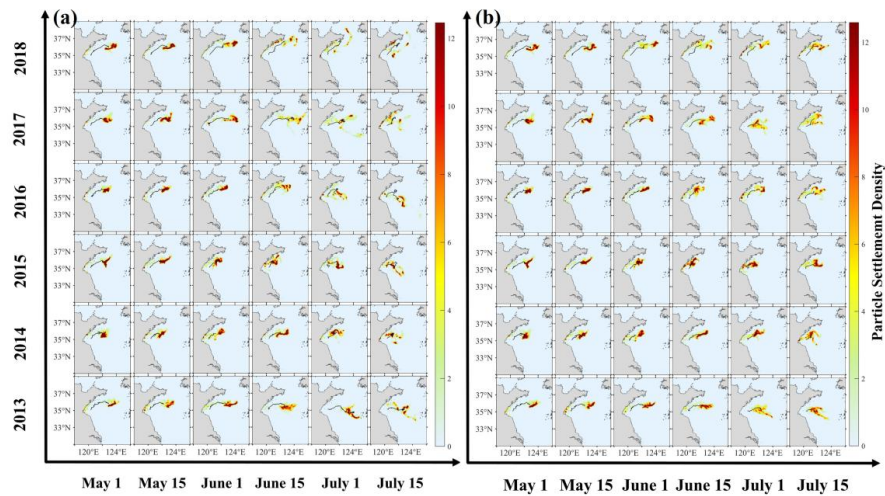


Figure 6. Spatial density distribution of settled larval particles released on different dates from different years, using the (a) Growing Degree-Days (GDD) approach, and (b) Optimal Growth Temperature (OGT) approach. Values shown on the color scale represent the relative particle density within each $0.025^{\circ} \times 0.025^{\circ}$ grid cell (approximately 6.3 km^2). The solid black lines represent the centroid trajectories of the dispersed larvae.

Table 1. The 6-year mean median-dispersal distance (MDD) and long-distance dispersal (LDD).

Approach	Release Date	6-Year Mean MDD (km)	6-Year Mean LDD (km)	6-Year Mean Travel duration (d)
GDD	May 1	226.5 ± 43.5	296.2 ± 44.3	62.1 ± 3.6
	May 15	215.5 ± 45.1	291.8 ± 42.1	50.7 ± 2.9
	June 1	210.9 ± 65.3	287.3 ± 76.2	40.7 ± 2.2
	June 15	181.4 ± 54.9	281.3 ± 69.6	34.4 ± 1.9
	July 1	162.1 ± 39.8	257.7 ± 66.4	28.8 ± 2.2
	July 15	154.2 ± 34.4	244.1 ± 43.4	25.5 ± 1.9
OGT	May 1	227.0 ± 45.4	295.7 ± 47.0	61.1 ± 4.2
	May 15	214.4 ± 44.7	291.0 ± 43.4	49.5 ± 2.9
	June 1	232.9 ± 83.5	302.8 ± 87.0	44.5 ± 1.3



	June 15	232.1 ± 78.8	339.0 ± 94.4	50.3 ± 9.8
	July 1	175.2 ± 66.0	324.5 ± 121.8	61.7 ± 10.0
	July 15	146.6 ± 53.2	287.5 ± 87.2	63.3 ± 7.2
30 d	May 1	128.2 ± 27.5	191.7 ± 30.4	--
	May 15	140.9 ± 42.5	212.7 ± 43.8	--
	June 1	152.3 ± 41.4	236.7 ± 50.8	--
	June 15	159.2 ± 54.0	250.2 ± 62.3	--
	July 1	160.3 ± 42.4	262.1 ± 68.7	--
	July 15	168.8 ± 41.0	260.6 ± 64.3	--

346 4. Discussion

347 4.1. Spawning Phenology Couples Physical Transport and Biological Development

348 Our results show that spawning phenology shapes larval dispersal through two coupled pathways:
 349 seasonal hydrodynamics determine transport velocity and direction, while trajectory-specific thermal
 350 histories regulate development and thus travel duration. Because circulation determines both larval
 351 trajectories and the temperatures experienced along them, physical transport and biological development
 352 are inherently linked. This trajectory–development coupling ultimately controls both how far and how
 353 long larvae are transported.

354 The fixed 30-d simulations provide a useful numerical baseline for separating these two pathways.
 355 When travel duration was held constant, median dispersal distance increased from 128.2 km for larvae
 356 released on May 1 to 168.8 km for those released on July 15, indicating progressively stronger effective
 357 hydrodynamic transport over the spawning season. In contrast, when travel duration was allowed to
 358 respond to trajectory-specific temperature under the GDD approach, travel duration declined from 62.1
 359 to 25.5 d and median dispersal distance declined from 226.5 to 154.2 km over the same release period.
 360 Thus, spawning-time effects on dispersal cannot be inferred from seasonal circulation alone because
 361 biological development modifies the amount of time over which that circulation can act.

362 This distinction has broader implications for biophysical dispersal modelling. Pelagic larval
 363 duration or, more generally, the duration of the dispersive stage is commonly prescribed as a fixed
 364 species-specific parameter in particle-tracking simulations. Such an approach is convenient, but it
 365 implicitly assumes that larvae released at different times and transported along different trajectories



366 develop at the same rate. Our results show that this assumption can break down when the thermal
 367 environment changes substantially across the spawning season. Treating travel duration as an
 368 environmentally responsive biological trait rather than as a fixed model parameter may therefore provide
 369 a more mechanistic representation of larval dispersal.

370 **4.2. Temperature-Dependent Development Can Counteract Seasonal Hydrodynamic Transport**

371 A central finding of this study is that temperature-dependent development can counteract, and in
 372 some cases reverse, the seasonal dispersal trend expected from hydrodynamics alone. Under the fixed
 373 30-d scenario, both MDD and LDD generally increased with later release dates, indicating that seasonal
 374 hydrodynamic conditions favored progressively greater displacement. Under the GDD approach,
 375 however, MDD and LDD decreased nearly monotonically with later spawning. Later-spawned larvae
 376 experienced warmer temperatures, developed more rapidly, and therefore remained exposed to advective
 377 transport for a substantially shorter period. The reduction in travel duration was sufficiently large to
 378 outweigh the simultaneous increase in hydrodynamic transport, producing a seasonal dispersal trend
 379 opposite to that predicted using a fixed travel duration. This result suggests that fixed-duration
 380 simulations may introduce not only a quantitative bias in estimated dispersal distance, but also a
 381 qualitative bias in the inferred seasonal response. This is particularly relevant for species with prolonged
 382 spawning seasons, for which larvae released only several weeks apart may experience substantially
 383 different thermal environments and developmental rates.

384 The OGT approach further demonstrates that the influence of temperature on dispersal depends on
 385 the shape of the thermal–development relationship. Whereas the GDD formulation assumes that
 386 development accelerates progressively with increasing thermal accumulation above a base temperature,
 387 the OGT formulation incorporates a thermal optimum, above which growth declines. Consequently,
 388 OGT-derived travel duration decreased from early May to early June but increased again as experienced
 389 temperatures exceeded the optimal range later in the season. This nonlinear response generated a more
 390 complex seasonal pattern in dispersal than the nearly monotonic response predicted by the GDD
 391 approach.

392 The difference between the two approaches should therefore not be interpreted simply as uncertainty
 393 over which model produces the more accurate travel duration. Rather, it highlights a more general
 394 ecological point: the response of larval dispersal to warming depends on the form of the underlying



395 thermal performance relationship. The frequently invoked expectation that warmer conditions accelerate
 396 development and shorten larval duration is likely to hold only when experienced temperatures remain
 397 below or near the rising portion of the thermal response curve. Once temperatures approach or exceed a
 398 physiological optimum, additional warming may produce little further acceleration or may even slow
 399 growth and prolong the period available for transport.

400 For Japanese anchovy in the Yellow Sea, the appropriate temperature–growth relationship remains
 401 uncertain. The OGT formulation was derived from field observations across the western North Pacific
 402 (Takasuka et al., 2007), whereas the GDD formulation represents cumulative thermal development and
 403 has been successfully applied across numerous fish populations (Neuheimer and Taggart, 2007). Our
 404 objective was therefore not to identify a single definitive growth model, but to test whether the effect of
 405 temperature-dependent development on dispersal is robust to alternative representations of thermal
 406 biology. The different responses obtained using GDD and OGT indicate that accurate characterization of
 407 species- and population-specific thermal performance will be essential for predicting dispersal under
 408 present and future temperature regimes. Laboratory and field measurements spanning the full range of
 409 temperatures experienced by Japanese anchovy larvae in the Yellow Sea would substantially reduce this
 410 uncertainty.

411 **4.3. Implications for Spawning Phenology, Spatial Match–Mismatch, and Population Connectivity**

412 Climate-driven shifts in spawning phenology are commonly considered in terms of temporal match–
 413 mismatch between larvae and their prey (Asch, 2015; Asch et al., 2019). Our results suggest an additional
 414 spatial dimension. By altering both seasonal circulation and trajectory-specific thermal histories,
 415 spawning-time shifts can change travel duration by several weeks and thus where larvae reach a given
 416 developmental stage. Phenological shifts may therefore alter not only when larvae encounter prey or
 417 suitable nursery habitat, but also where these encounters occur. Because prey and habitat suitability were
 418 not explicitly modeled, this spatial match–mismatch remains a hypothesis rather than a demonstrated
 419 recruitment response.

420 Temperature-dependent travel duration may also affect population connectivity by changing the
 421 time available for larvae to leave spawning grounds or reach distant habitats. Fixed-duration models may
 422 therefore misrepresent dispersal and spawning–nursery connectivity, with potential consequences for
 423 local retention and recruitment. Under climate change, these effects will depend on how shifts in



424 spawning phenology and warming modify seasonal circulation and larval development. Incorporating
 425 temperature-dependent development may thus improve connectivity predictions, particularly for species
 426 with prolonged spawning seasons and strong seasonal temperature variability.

427 **4.4. Model Uncertainties and Future Directions**

428 Several limitations should be considered when interpreting the present simulations. (1) Larvae were
 429 represented as passive particles. Japanese anchovy larvae develop swimming ability during ontogeny,
 430 and directional swimming, or other active behaviours could modify their horizontal trajectories. The
 431 present simulations should therefore be interpreted as a mechanistic baseline designed to isolate the
 432 coupled effects of hydrodynamic transport and temperature-dependent development rather than as a
 433 complete prediction of realized larval distributions. (2) larvae were constrained to the surface layer
 434 without diel or ontogenetic vertical migration, which could alter both the currents and temperatures
 435 experienced and thus affect transport and development. These assumptions provide a simplified
 436 mechanistic baseline for isolating hydrodynamic and temperature-dependent effects, consistent with
 437 previous Japanese anchovy transport studies (Takeshige et al., 2015; Xing et al., 2021; Xing et al., 2020).
 438 (3) Temperature was treated as the primary environmental control on growth, whereas larval
 439 development in nature is also influenced by prey availability, food quality, physiological condition,
 440 predation risk, and other environmental factors. The development models used here should therefore be
 441 interpreted as deliberately isolating the thermal pathway rather than reproducing all controls on realized
 442 larval growth. (4) Uncertainty remains in the parameterization of temperature-dependent development.
 443 The GDD threshold was derived from available laboratory information, whereas the OGT relationship
 444 was based on field observations from a broader western North Pacific region. Neither relationship has
 445 been comprehensively validated for Japanese anchovy larvae in the Yellow Sea. Nevertheless, using two
 446 contrasting formulations was useful because both showed that allowing travel duration to respond to
 447 thermal history substantially altered predicted dispersal relative to a fixed-duration assumption, while
 448 their differences revealed the sensitivity of dispersal to the form of the thermal–development relationship.

449 Despite these limitations, the central mechanism identified here is robust: spawning phenology can
 450 simultaneously modify the physical rate of larval transport and the biologically determined duration over
 451 which transport occurs. These two effects need not act in the same direction. In the present simulations,
 452 temperature-dependent development was sufficiently strong to counteract and even reverse the seasonal



453 dispersal trend expected from hydrodynamics alone. More generally, our results suggest that larval travel
 454 duration should be treated as an environmentally responsive component of biophysical dispersal rather
 455 than as a fixed parameter, particularly when evaluating seasonal variability or climate-driven shifts in
 456 spawning phenology.

457 **Code and data availability**

458 The particle tracking code and simulated data are available through Zenodo ([10.5281/zenodo.21358003](https://doi.org/10.5281/zenodo.21358003)).

459 **Author Contributions**

460 YFD: Data Curation; Formal Analysis; Investigation; Software; Visualization; Writing - Original Draft
 461 Preparation.

462 WS: Conceptualization; Formal Analysis; Methodology; Supervision; Writing – Review & Editing.

463 SJC: Funding Acquisition; Review & Editing.

464 LB: Review & Editing.

465 YJT: Funding Acquisition; Project Administration; Resources; Software; Supervision; Review & Editing.

466 **Conflict of Interest**

467 The authors declare that they have no conflict of interest.

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473 **References**

- 474 Almany, G. R., Planes, S., Thorrold, S. R., Berumen, M. L., Bode, M., Saenz-Agudelo, P., Bonin, M. C.,
 475 Frisch, A. J., Harrison, H. B., Messmer, V., Nanninga, G. B., Priest, M. A., Srinivasan, M., Sinclair-Taylor,
 476 T., Williamson, D. H., and Jones, G. P.: Larval fish dispersal in a coral-reef seascape, *Nat Ecol Evol*, 1,
 477 148, 10.1038/s41559-017-0148, 2017.
 478 Asch, R. G.: Climate change and decadal shifts in the phenology of larval fishes in the California Current
 479 ecosystem, *Proc Natl Acad Sci U S A*, 112, E4065-4074, 10.1073/pnas.1421946112, 2015.
 480 Asch, R. G., Stock, C. A., and Sarmiento, J. L.: Climate change impacts on mismatches between
 481 phytoplankton blooms and fish spawning phenology, *Glob Chang Biol*, 25, 2544-2559,
 482 10.1111/gcb.14650, 2019.



- 483 Ayata, S. D., Lazure, P., and Thiébaud, É.: How does the connectivity between populations mediate range
484 limits of marine invertebrates? A case study of larval dispersal between the Bay of Biscay and the English
485 Channel (North-East Atlantic), *Prog. Oceanogr.*, 87, 18-36, 10.1016/j.pocean.2010.09.022, 2010.
- 486 Béguer-Pon, M., Shan, S., Thompson, K. R., Castonguay, M., Sheng, J., and Dodson, J. J.: Exploring the
487 role of the physical marine environment in silver eel migrations using a biophysical particle tracking
488 model, *ICES J. Mar. Sci.*, 73, 57-74, 10.1093/icesjms/fsv169, 2016.
- 489 Burgess, S. C., Bode, M., Leis, J. M., and Mason, L. B.: Individual variation in marine larval-fish
490 swimming speed and the emergence of dispersal kernels, *Oikos*, 2022, 10.1111/oik.08896, 2021.
- 491 Chaput, R., Sochala, P., Miron, P., Kourafalou, V. H., Iskandarani, M., and Kaplan, D. M.: Quantitative
492 uncertainty estimation in biophysical models of fish larval connectivity in the Florida Keys, *ICES J. Mar.*
493 *Sci.*, 79, 609-632, 10.1093/icesjms/fsac021, 2022.
- 494 Cowen, R. K. and Sponaugle, S.: Larval Dispersal and Marine Population Connectivity, *Annual Review*
495 *of Marine Science*, 1, 443-466, 10.1146/annurev.marine.010908.163757, 2009.
- 496 Faillietaz, R., Paris, C. B., and Irisson, J.-O.: Larval Fish Swimming Behavior Alters Dispersal Patterns
497 From Marine Protected Areas in the North-Western Mediterranean Sea, *Frontiers in Marine Science*, 5,
498 10.3389/fmars.2018.00097, 2018.
- 499 Hinrichsen, H.-H., Kühn, W., Peck, M. A., and Voss, R.: The impact of physical and biological factors
500 on the drift and spatial distribution of larval sprat: A comparison of the Baltic and North Seas, *Prog.*
501 *Oceanogr.*, 107, 47-60, 10.1016/j.pocean.2012.05.004, 2012.
- 502 Huret, M., Petitgas, P., and Woillez, M.: Dispersal kernels and their drivers captured with a hydrodynamic
503 model and spatial indices: A case study on anchovy (*Engraulis encrasicolus*) early life stages in the Bay
504 of Biscay, *Prog. Oceanogr.*, 87, 6-17, 10.1016/j.pocean.2010.09.023, 2010.
- 505 Iseki, K. and Kiyomoto, Y.: Distribution and settling of Japanese anchovy (*Engraulis japonicus*) eggs at
506 the spawning ground off Changjiang River in the East China Sea, *Fisheries Oceanography*, 6, 205-210,
507 10.1046/j.1365-2419.1997.00040.x, 1997.
- 508 Lett, C., Verley, P., Mullon, C., Parada, C., Brochier, T., Penven, P., and Blanke, B.: A Lagrangian tool
509 for modelling ichthyoplankton dynamics, *Environmental Modelling & Software*, 23, 1210-1214,
510 10.1016/j.envsoft.2008.02.005, 2008.
- 511 Lu, J., Chen, Y., Wang, Z., Zhao, F., Zhong, Y., Zeng, C., and Cao, L.: Larval Dispersal Modeling Reveals
512 Low Connectivity among National Marine Protected Areas in the Yellow and East China Seas, *Biology*,
513 12, 10.3390/biology12030396, 2023.
- 514 Majoris, J. E., Catalano, K. A., Scolaro, D., Atema, J., and Buston, P. M.: Ontogeny of larval swimming
515 abilities in three species of coral reef fishes and a hypothesis for their impact on the spatial scale of
516 dispersal, *Mar. Biol.*, 166, 10.1007/s00227-019-3605-2, 2019.
- 517 Masuda, R.: Ontogeny of swimming speed, schooling behaviour and jellyfish avoidance by Japanese
518 anchovy *Engraulis japonicus*, *J Fish Biol.*, 78, 1323-1335, 10.1111/j.1095-8649.2011.02936.x, 2011.
- 519 Neuheimer, A. B. and Taggart, C. T.: The growing degree-day and fish size-at-age: the overlooked metric,
520 *Canadian Journal of Fisheries and Aquatic Sciences*, 64, 375-385, 10.1139/f07-003, 2007.
- 521 O'Connor, M. I., Bruno, J. F., Gaines, S. D., Halpern, B. S., Lester, S. E., Kinlan, B. P., and Weiss, J. M.:
522 Temperature control of larval dispersal and the implications for marine ecology, evolution, and
523 conservation, *Proc Natl Acad Sci U S A*, 104, 2007.
- 524 Saito, N., Kise, H., Nakajima, Y., and Iguchi, A.: Kuroshio Corridor: larval dispersal networks explain
525 geographically independent connectivity among coral habitats in Japan, *Sci Rep*, 16, 10.1038/s41598-
526 026-40448-z, 2026.



- 527 Sato, M., Honda, K., Nakamura, Y., Bernardo, L. P. C., Bolisay, K. O., Yamamoto, T., Herrera, E. C.,
528 Nakajima, Y., Lian, C., Uy, W. H., Fortes, M. D., Nadaoka, K., and Nakaoka, M.: Hydrodynamics rather
529 than type of coastline shapes self-recruitment in anemonefishes, *Limnology and Oceanography*, 69,
530 10.1002/lno.12399, 2023.
- 531 Shi, L. and Zhao, Q.: Temporal and spatial variation characteristics and influence mechanism of surface
532 cold water in the North Yellow Sea in summer, *Marine Environment Science*, 45, 136-144, 155,
533 10.3724/j.1007-6336.2025-0077, 2026.
- 534 Shi, W., Boegman, L., Ackerman, J. D., Shan, S., and Zhao, Y.: Computation of fish larvae self-
535 recruitment in using forward- and backward-in-time particle tracking in a Lagrangian model (SWIM-
536 v2.0) of the simulated circulation of Lake Erie (AEM3D-v1.1.2), *Geoscientific Model Development*, 19,
537 1213-1228, 10.5194/gmd-19-1213-2026, 2026a.
- 538 Shi, W., Boegman, L., Ackerman, J. D., Shan, S., Yang, T., Chong, K. J., and Zhao, Y.: A Growing
539 Degree-Day Approach to Estimate Larval Hatching Sites Using Backtracking Simulations Without
540 Larval Age, *Journal of Geophysical Research: Biogeosciences*, 131, 10.1029/2025jg009299, 2026b.
- 541 Shi, W., Boegman, L., Shan, S., Ackerman, J. D., Chong, K. J., Zhao, Y., and Kaplan, D. M.: Positive
542 rheotaxis increases settlement success of walleye (*Sander vitreus*) larvae in western Lake Erie, *ICES J.*
543 *Mar. Sci.*, 83, 10.1093/icesjms/fsag116, 2026c.
- 544 Shi, W., Boegman, L., Shan, S., Zhao, Y., Ackerman, J. D., Amidon, Z., Jabbari, A., and Roseman, E.: A
545 Larval “Recruitment Kernel” to Predict Hatching Locations and Quantify Recruitment Patterns, *Water*
546 *Resources Research*, 60, 10.1029/2023wr036099, 2024.
- 547 Shi, W., Boegman, L., Shan, S., Tian, Y., Liu, Y., Sun, P., Ye, Z., Xing, Q., and Li, J.: Quantifying patterns
548 and drivers of larval dispersal in Japanese anchovy (*Engraulis japonicus*) in the China Seas,
549 *Biogeosciences*, 23, 6003-6018, 10.5194/bg-23-6003-2026, 2026d.
- 550 Suhaemi, Apriansyah, Raharjo, S., Sembel, L., Kusuma, A. B., and Marhan: Numerical study of three-
551 dimensional circulation and virtual grouper larval dispersal in Cenderawasih Bay, Indonesia, *Regional*
552 *Studies in Marine Science*, 96, 10.1016/j.rsma.2026.104909, 2026.
- 553 Takasuka, A., Oozeki, Y., and Aoki, I.: Optimal growth temperature hypothesis: Why do anchovy flourish
554 and sardine collapse or vice versa under the same ocean regime?, *Canadian Journal of Fisheries and*
555 *Aquatic Sciences*, 64, 768-776, 10.1139/f07-052, 2007.
- 556 Takeshige, A., Miyake, Y., Nakata, H., Kitagawa, T., and Kimura, S.: Simulation of the impact of climate
557 change on the egg and larval transport of Japanese anchovy (*Engraulis japonicus*) off Kyushu Island, the
558 western coast of Japan, *Fisheries Oceanography*, 24, 445-462, 10.1111/fog.12121, 2015.
- 559 Togoshi, S., Tanaka, S., Yasue, N., Nakamura, M., Robert, D., and Takasuka, A.: Growth–feeding linkage
560 in small pelagic fish larvae in the Kii Channel, Japan, *Fisheries Oceanography*, 33, 10.1111/fog.12678,
561 2024.
- 562 Wood, S., Paris, C. B., Ridgwell, A., and Hendy, E. J.: Modelling dispersal and connectivity of broadcast
563 spawning corals at the global scale, *Global Ecology and Biogeography*, 23, 1-11, 10.1111/geb.12101,
564 2013.
- 565 Xing, Q., Yu, H., Yu, H., Sun, P., Liu, Y., Ye, Z., Li, J., and Tian, Y.: A comprehensive model-based index
566 for identification of larval retention areas: A case study for Japanese anchovy *Engraulis japonicus* in the
567 Yellow Sea, *Ecological Indicators*, 116, 10.1016/j.ecolind.2020.106479, 2020.
- 568 Xing, Q., Yu, H., Ito, S.-i., Ma, S., Yu, H., Wang, H., Tian, Y., Sun, P., Liu, Y., Li, J., and Ye, Z.: Using a
569 larval growth index to detect the environment–recruitment relationships and its linkage with basin-scale
570 climate variability: A case study for Japanese anchovy (*Engraulis japonicus*) in the Yellow Sea,



571 Ecological Indicators, 122, 10.1016/j.ecolind.2020.107301, 2021.
572 Zhang, W., Ye, Z., Tian, Y., Yu, H., Ma, S., Ju, P., and Watanabe, Y.: Spawning overlap of Japanese
573 anchovy *Engraulis japonicus* and Japanese Spanish mackerel *Scomberomorus niphonius* in the coastal
574 Yellow Sea: A prey–predator interaction, *Fisheries Oceanography*, 31, 456–469, 10.1111/fog.12595, 2022.
575 Zhang, W., Yu, H., Ye, Z., Tian, Y., Liu, Y., Li, J., Xing, Q., and Jiang, Y.: Spawning strategy of Japanese
576 anchovy *Engraulis japonicus* in the coastal Yellow Sea: Choice and dynamics, *Fisheries Oceanography*,
577 30, 366–381, 10.1111/fog.12523, 2020.
578 Zhao, X., Hamre, J., Li, F., Jin, X., and Tang, Q.: Recruitment, sustainable yield and possible ecological
579 consequences of the sharp decline of the anchovy (*Engraulis japonicus*) stock in the Yellow Sea in the
580 1990s, *Fisheries Oceanography*, 12, 495–501, 10.1046/j.1365-2419.2003.00262.x, 2003.
581